THE DESOXYRIBONUCLEIC ACID CONTENT OF THE NUCLEUS AS A CYTOTAXONOMIC CHARACTER IN MANTIDS (ORTHOPTERA: MANTOIDEA)

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The hypothesis that the nuclear content of desoxyribonucleic acid is a constant character of the species is supported by rapidly accumulating evidence (Boivin, Vendrely and Vendrely, 1948; Vendrely and Vendrely, 1948, 1949, 1950; Mirsky and Ris, 1949; Ris and Mirsky, 1949; Swift, 1950a, 1950b; and others). It moreover appears probable that the higher taxonomic categories will show a characteristic order of magnitude with respect to this value; and polyploid species already tested show the expected stepwise relation. The possibility is thus opened that the amount of DNA per nucleus may prove a useful cytotaxonomic tool in evaluating evolutionary relationships among species whose karyotypes are not analyzable by the methods of comparative cytology. The following report records a preliminary exploration of this possibility for certain problems of karyotype relationship among mantids.

Cytological Background

The first group investigated comprises three species of the taxonomically difficult genus *Liturgousa* of the subfamily Liturgousinae. Closely similar in phenotype and habit, and occupying common or adjacent ranges, they differ widely in chromosome complements (Hughes-Schrader, 1950). *L. maya* has 16 autosomes, while *L. cursor* precisely doubles this number with 32, and *L. actuosa* [1] is intermediate with 22. While the X chromosome appears identical in all three, the autosomes are not morphologically homologous, but show in general an inverse relation of size to number (Figs. 1, 2 and 3). No direct Robertsonian relation (the evolutionary equivalence of one mediokinetic to two acrokinetic chromosomes) is demonstrable between *L. maya* and *L. actuosa*, nor between *L. maya* and *L. cursor*. It is possible, however, that *L. cursor* and *L. actuosa* stand in this relation to each other, if the 10 pairs of apparently rod-shaped autosomes of the former correspond to 5 pairs of V-shaped elements in the latter. No final conclusion is justified since the position of the kinetochore in the short chromosomes of *L. cursor* cannot be established positively. On comparative inspection the chromosomes of the three species appear approximately equal in total mass, but measurement at spermatogonial metaphase shows the total length of the chromosomes to vary inversely with chromosome number (Table I). The total cytological evidence thus fails to make clear the evolutionary relationship of these species. While precluding polyploidy, it suggests

[1] The erroneous name *L. arcuosa* was used for this species by Hughes-Schrader (1950). Its correct designation and description have since then become available in Rehn, 1951, *Trans. Ent. Soc.* **76**: 363–383.

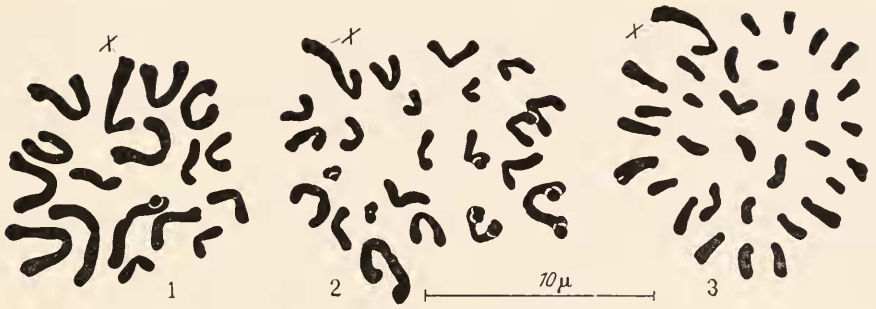

FIGURE 1. Spermatogonial metaphase—*Liturgousa maya.*
FIGURE 2. Same—*Liturgousa actuosa.*
FIGURE 3. Same—*Liturgousa cursor.*

(All drawings made with camera lucida, at table level; Zeiss apochrom. obj. 90, comp. oc. 20; magnification as reproduced is uniform in all and indicated by scale on each. Fixation Sanfelice; stain Feulgen.)

that changes in total amount of chromosome material, as well as changes in its distribution and in number of kinetochores, have been associated with this divergence. Measurement of metaphase chromosomes in any species can, however, at best give but an approximate index of the amount of chromosome material, for differences in intensity of dye and tightness of coiling cannot be adequately appraised. It was therefore hoped that the photometric determination of the relative amount of DNA in the interphase nucleus, by providing a more accurate index of the substance measured in Feulgen-dyed metaphase chromosomes, might elucidate the interrelationship of the *Liturgousa* species.

With the dual purpose, first, of providing a standard of comparison for possible interspecific differences in the nuclear DNA content among the *Liturgousa* species, and second, of ascertaining whether or not cytotaxonomically useful constants of nuclear DNA content characterize different subfamilies, measurements were also made on a second group of mantids from the very distantly related subfamily Manteinae. These were chosen on the basis of close similarity in karyotype, and include

TABLE I

Average total length, in arbitrary units, of metaphase chromosomes

Species	Chromosomes 2n ♂	Spermatogonia	Number measured	Meiosis II	Number measured
Liturgousa maya	16+X	59.9	3		
Liturgousa cursor	32+X	42.6	3		
Liturgousa actuosa	22+X	51.5	3		
Choeradodis rhombicollis	28+X^1X^2Y	56.3	3		
Stagmomantis carolina	24+X^1X^2Y	62.5	4	53.6	4
Stagmomantis heterogamia	24+X^1X^2Y	68.2*		58.6	6
Tauromantis championi	24+X^1X^2Y	66.0	5		
Pseudomiopteryx infuscata	16+X	26.9*		23.1	8

* Calculated from ratio of total length of meiotic to gonial chromosomes in *Stagmomantis carolina.*

Tauromantis championi, Stagmomantis carolina, and *Stagmomantis heterogamia* (Figs. 4, 5 and 7). The chromosome number ($2n♂$) is 27 in each, comprising 12 pairs of autosomes and the compound sex chromosomes X^1, X^2 and Y; the chromosomes are similar in size, with the exception of the Y chromosome, which is identical in the *Stagmomantis* species but considerably larger in *Tauromantis* (Hughes-Schrader, 1950).

Of special interest would be a comparison of DNA nuclear content between *Choeradodis* and the Manteinae. The genus is currently elevated to separate subfamily rank, but *Choeradodis rhombicollis* is shown by the cytological evidence provided by the morphology and behavior of the compound sex chromosomes to stand in closer relation to the X^1X^2Y Manteinae than is recognized taxonomically (Hughes-Schrader, 1950). The autosomes of *Choeradodis,* while numbering two more pairs than are found in the Manteinae, are individually considerably smaller and their total length appears approximately the same as in the latter. Unfortunately, the only

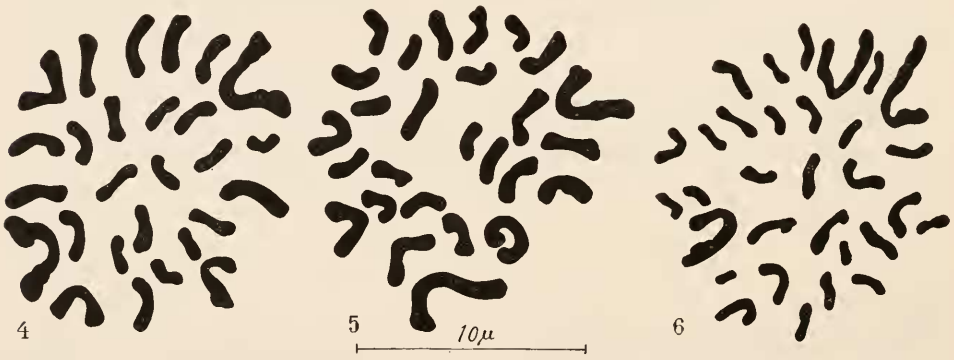

FIGURE 4. Spermatogonial metaphase—*Stagmomantis carolina.*
FIGURE 5. Same—*Tauromantis championi.*
FIGURE 6. Same—*Choeradodis rhombicollis.*

material of *Choeradodis* available for photometry gives evidence of considerable cytological abnormality; the results obtained from it can be regarded as suggestive only.

Finally, measurements were made on nuclei of *Pseudomiopteryx infuscata* of the subfamily Pseudomiopteriginae. Here, while the chromosome number ($2n♂ = 17$) is the same as in *Liturgousa maya,* the total mass of the chromosomes appears to be far less. When compared with the manteine species *Stagmomantis heterogamia,* the total length of the chromosomes of the *Pseudomiopteryx* complement is seen to be less than half that in the first named species (Table I and Figs. 7 and 8). The nuclear DNA content of such a karyotype is of special interest since the distribution of chromosome numbers among all cytologically known mantids shows two peaks—a dominant one at 27 with outlying species ranging upwards to 39, and a secondary peak embracing the 15 to 19 chromosome range. Furthermore, in many of the high-number karyotypes the X chromosome (or its derivative arms in X^1 and X^2) is of extreme length relative to the autosomes and in comparison with the X of certain low-number karyotypes such as that of *Pseudomiopteryx.* Thus, the

possibility exists that polyploidy—its establishment made possible by the stabilization of the sex chromosome mechanism through fusion of the X chromosomes, along lines similar to those first postulated by Bauer (1947) for certain Dermaptera—has been involved in the evolution of the Mantoidea. Of course no implication of any recently established diploid to tetraploid relation between *Pseudomiopteryx* and *Stagmomantis* is intended; taxonomic and cytologic considerations alike preclude it. They were chosen, from the limited material available, as roughly representative in general features of chromosomal mass, number, and morphology of the postulated ancestral karyotypes.

Material and Methods

The material used comprises testes from males of the 8 species enumerated above; collection and field notes have been recorded previously (Hughes-Schrader,

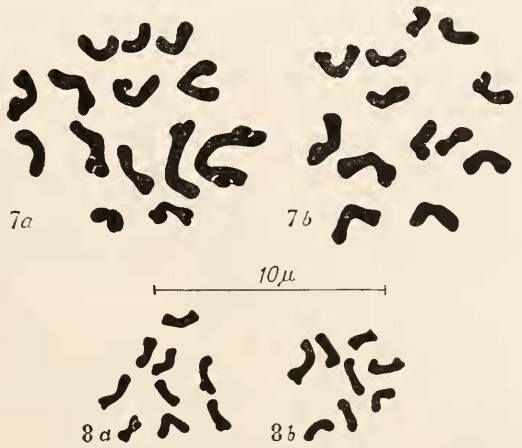

Figure 7. Second meiotic metaphase—*Stagmomantis heterogamia*. a. Secondary spermatocyte with X^1 and X^2; b. Secondary spermatocyte with Y.
Figure 8. Second meiotic metaphase—*Pseudomiopteryx infuscata*. a. Secondary spermatocyte with X; b. Secondary spermatocyte with no X.

1950). For photometric measurements two individuals of each of the three species of *Liturgousa,* and one of each of the other 5 species, were used. The material was fixed in Sanfelice, washed in water overnight, embedded in paraffin and sectioned at 8 or 10 μ. Sections from each of the *Liturgousa* species were mounted together on consecutive slides, as were those of the Manteinae-*Choeradodis* group. In addition the slides of the latter series carried sections from one testis of the first group to provide a standard for comparison of data from different slides. The limited material available restricted direct comparison of *Pseudomiopteryx* to *Stagmomantis heterogamia* and *Choeradodis* of the second group.

Staining was by the Feulgen method; alternate slides in each series constituted unhydrolyzed controls. The photometric measurements were made by the Pollister and Ris (1947) method and with the apparatus described by Swift (1950a). DNA in the nucleus was measured as the extinction of the Feulgen dye at the 546 mμ line, isolated by a Farrand Interference Filter No. 2756 from an AH4 mercury

vapor lamp. The relative amount of DNA per nucleus was calculated in arbitrary units of Feulgen dye, according to the formulae given by Swift (1950a): the measured extinction of a cylinder 3.8 μ in diameter through an uncut nucleus is multiplied by the squared radius of the cylinder and divided by the percentage of the total nuclear volume represented by the cylinder. The nuclei measured deviated only slightly if at all from the spherical; major and minor axes were measured and the mean considered as the diameter. Feulgen preparations following Sanfelice fixation of mantid testes often show, in control and test slide alike, a diffuse stain in the cytoplasm. Since the intensity of this cytoplasmic dye varied significantly among some of the species tested, the extinction of each nucleus measured was corrected by a factor relating the amount of overlying cytoplasm to the cytoplasmic extinction.

Spermatid nuclei were chosen for measurement since they may be expected to be relatively free of variation in DNA associated either with mitosis or with special metabolic function. Moreover, throughout the series of species tested, spermatid nuclei proved highly comparable morphologically. Fortunately also, in all these species, the chromosomes continue to de-spiralize after the second meiotic telophase and, just prior to the elongation of the nucleus to form the head of the sperm, they reach a state of relatively extreme extension and rather diffuse staining which is favorable for photometric measurements. To avoid variation stemming from differential penetration effects, only nuclei from cysts at or very close to the surface of the testis were utilized. All testes used, with the exception of the *Choeradodis* material, are from nymphal males and provide an abundance of uniform, normal-appearing spermatid nuclei of the desired stage. The only available material of *Choeradodis* comes from an adult male with spent testes. Only a few cysts of the required stage of spermatid are present; and these give evidence—through wide variation in nuclear size and stain and a high frequency of giant and micro nuclei—of abnormality in chromosome distribution in the preceding mitosis.

To facilitate correlation of the photometric data with the cytological findings, estimates were made of the total length of the chromosomes at spermatogonial or second meiotic metaphase in Feulgen preparations. It was found that a reasonable agreement in values was obtained only from the relatively few plates in which all chromosomes were extended fairly flatly in one plane; the figures on total length in Table I are the mean values from measurements of from three to eight such metaphase plates. The maximum deviation from the average did not exceed 8 per cent, except in *Tauromantis* and *Choeradodis* plates, where it reached 14 per cent. Camera lucida drawings, at 1800 ×, were enlarged four fold by pantograph and the length of each chromosome recorded with a map measure. It proved impossible to gauge the diameter of the chromosome satisfactorily by this method; and since differences in chromosome diameter are distinguishable among these species, the total chromosome length can give only an approximation of total mass.

Results

The photometric measurements of the relative amount of DNA in spermatid nuclei disclose a range of values characteristic for each of the species tested. The results are summarized in Table II, in which each major vertical column contains data from a single slide. For brevity in presentation the results are recorded as the

mean values of the different samples of nuclei measured. The use of the mean DNA per nucleus value as a species constant appears justified for purposes of preliminary interspecific comparison; to what extent the spread of values about the mean reflects real variation among the nuclei, and to what extent errors in method and measurement, is unknown. The pattern of scatter of the values obtained does show the effect of the segregation of the sex chromosomes, especially in the spermatids of the manteine species where two relatively large X chromosomes have segregated from a small Y. When DNA content is plotted against number of nuclei, some indication of a bimodal distribution is apparent in each sample. It is also of interest to note, relative to the variation within the species range, that no nucleus measured contains DNA in an amount equal to or closely approaching twice the mean value, and in only four instances was the maximum value twice that of the minimum obtained.

TABLE II

Average amounts (in arbitrary units of Feulgen dye) of DNA in spermatid nuclei of mantid species. (a,b = 2 individuals tested; N = number of nuclei measured)

Species	Slide 1			Slide 2			Slide 3			Slide 4			Slide 5			Total number of nuclei measured
	DNA	S.E.	N	DNA	S.E.	N	DNA	S.E.	N	DNA	S.E.	N	DNA	S.E.	N	
Liturgousa maya a	1.11	0.041	14	1.04	0.049	16										30
Liturgousa maya b				1.06	0.026	15										15
Liturgousa cursor a	1.01	0.026	10	0.98	0.027	15										25
Liturgousa cursor b										1.04	0.029	20				20
Liturgousa actuosa a	1.51	0.041	15	1.48	0.049	16	1.50	0.059	12	1.43	0.025	20				63
Liturgousa actuosa b										1.65	0.020	20				20
Choeradodis rhombicollis							1.52	0.086	20				1.18	0.027	36	56
Stagmomantis carolina							1.80	0.073	20							20
Stagmomantis heterogamia							1.65	0.060	20				1.59	0.041	26	46
Tauromantis championi							1.73	0.077	17							17
Pseudomiopteryx infuscata													0.74	0.024	20	20

Before turning to a consideration of the results in relation to the cytological problems presented, one other point of general interest should be emphasized. As shown in Table II (slides 2 and 4), the two individuals of *Liturgousa maya* tested are practically identical in respect to the DNA content of spermatid nuclei; the same is true of the two specimens of *L. cursor*. In *L. actuosa,* however, a significant difference is apparent (Table II, slide 4)—the second individual tested shows a value 15 per cent higher than that of the first. In view of this finding, the number of individuals of each species sampled in the present study must be considered as too low to justify final conclusions as to the limits of the specific range in the DNA value of the spermatid.

DISCUSSION

Liturgousinae

In the three species of *Liturgousa* studied, it is clear (Table II, slides 1 to 4) that the amount of DNA per spermatid nucleus does not vary directly with chromosome number and size. The nuclei (haploid) of *L. maya* with 8 autosomes and

those of *L. cursor* with precisely twice as many show no significant difference in DNA content. This is in agreement with the tentative conclusion based on cytological data (Hughes-Schrader, 1950) that a re-distribution of chromosome material and a change of kinetochore number not involving polyploidy has been associated with the evolutionary divergence of these species. In view of the 1 : 1 ratio in DNA it is, however, surprising to find a ratio of 1.4 : 1 in the total length of metaphase chromosomes between *L. maya* and *L. cursor* (Table I) ; moreover, the *L. maya* chromosomes are appreciably thicker than those of *L. cursor.* This discrepancy may be more apparent than real in respect to the actual amount of Feulgen-positive material present, since considerable differences in intensity of stain and in degree of condensation of the metaphase chromosomes are not detectable by the eye.

But by far the most interesting result of the comparison of the *Liturgousa* species, and one not to be anticipated from the cytological evidence, is the wide divergence in DNA values of *L. actuosa* from its two sister species. Closely similar to *L. maya* and *L. cursor* in phenotype, intermediate between them in chromosome number and size and in total chromosome length, *L. actuosa* is characterized by an amount of DNA per spermatid which is half again as large as theirs. No differential polyteny among the chromosomes is discernible at the mitosis preceding spermatid formation; and in chromosome diameter—admittedly difficult to gauge with accuracy—*L. actuosa* appears to be intermediate between *L. maya* and *L. cursor.* That a change of such magnitude in the relative amount of DNA per nucleus may be effected among closely related species without a corresponding visible change in total chromosomal mass is, aside from its interest relative to chromosome structure, prejudicial to the hope that a DNA species constant will prove cytotaxonomically useful. The significance of this finding is of course dependent on the validity of my assumption that the spermatid nuclei of the species concerned are actually as comparable in respect to the timing of DNA synthesis as they appear to be in all cytologically demonstrable characters. If any synthesis, possibly anticipatory of the next mitosis, takes place in the spermatid nucleus, it may well have undergone interspecific variation in time or rate. It is thus desirable that the DNA content of the spermatid be compared to that of somatic nuclei in each of the species involved; unfortunately, this must await the collection of further material.

Manteinae

Uniformity in spermatid DNA characterizes the three species of the subfamily Manteinae—*Tauromantis championi, Stagmomantis carolina,* and *Stagmomantis heterogamia;* the mean values obtained (Table II, slide 3) do not differ significantly, and in range of values the four samples of nuclei measured are practically identical. This is in harmony with the cytological findings, for these species have the same number of chromosomes and are closely similar in chromosome morphology and behavior. In total length of chromosomes as measured at spermatogonial metaphase also, *Tauromantis* and *Stagmomantis carolina* are in good agreement (Table I). No measurable spermatogonial metaphases are available for *Stagmomantis heterogamia,* but at second meiotic metaphase the total length of its chromosomes agrees, within the probable error of measurement, with that of *S. carolina.* Assuming the same ratio in length between meiotic and gonial chromosomes in the

two *Stagmomantis* species, the total chromosome length at spermatogonial metaphase in the three manteines (Table I) shows no greater variation than is obtained in measurements of different plates in one species.

Relationships among X^1 X^2 Y mantids

The species of the subfamily Manteinae characterized by the compound sex chromosomes—X^1X^2Y ♂—$X^1X^1X^2X^2$ ♀—form a closely linked natural group cytologically—their joint possession of this particular sex chromosome mechanism denotes, with a high degree of probability, their descent from a single ancestral species (White, 1941). Species with a sex trivalent strikingly similar in structure and behavior are now known in four other subfamilies, and the cytological evidence indicates a closer relation to the Manteinae than is expressed in their taxonomic placement (Hughes-Schrader, 1950). Of these non-manteine X^1X^2Y species, material of only one—*Choeradodis rhombicollis*—was available for comparison of DNA values with the Manteinae. And as noted above, the few cysts of spermatids remaining in this adult testis give evidence of abnormalities in chromosome distribution in the preceding mitosis, which precludes a determinaton of the DNA constant of the species. The mean value for DNA in the spermatid in the two disparate samples measured, however, falls below that of the Manteinae (Table II, slides 3 and 5) ; and since not one nucleus in 56 measured exceeded in DNA the maximum value obtained in the Manteinae, we may expect the real value for *Choeradodis* to be somewhat lower than the general manteine level. This is of interest since *Choeradodis* has two more pairs of autosomes than is characteristic for X^1X^2Y Manteinae. The cytological evidence also indicates that the difference in chromosome number implies no increase in chromosome mass, for the total length of the spermatogonial chromosomes is approximately the same (Table I), and their diameter is appreciably less (Figs. 4, 5 and 6), than in the manteine species. As to the major issue, however—the relationship of X^1X^2Y species currently referred to different subfamilies—more normal material of *Choeradodis* than presently available is obviously necessary in order to test the relevancy of photometric data on nuclear DNA.

Polyploidy

Pseudomiopteryx of the subfamily Pseudomiopteriginae was chosen for photometric measurement of nuclear DNA content because, as noted previously, it represents a group of low-number karyotypes among mantids which apparently contain not more than half the Feulgen-positive chromosome material present in many high-number karyotypes such as the three species of the subfamily Manteinae here tested. This in turn suggests that polyploidy may have been involved in the early differentiation of high and low chromosome numbers in ancestral mantid stocks. The photometric data (Table II, slide 5) do indeed support this suggestion: the relative amounts of DNA per spermatid in *Pseudomiopteryx* as compared with *Stagmomantis heterogamia* closely approach a 1 : 2 ratio (ratio = 0.47). A greater disparity is apparent in total length of chromosomes at the last preceding mitosis (Table I) ; the ratio here is 0.39. Since, however, the arms of second meiotic metaphase chromosomes of both species tend to curl at the tips and the resulting error in measurement is proportionately greater in the shorter chromosomes of *Pseudomiopteryx,* this finding need not be considered wholly out of line with the photo-

metric data. On the other hand, the difference in diameter between the chromosomes of *Stagmomantis* and *Pseudomiopteryx,* as shown in Figures 7 and 8, gives the impression of a greater disparity in total mass than is indicated by the ratio in total length.

I am convinced that polyploidy has played a greater role in the evolution of animal karyotypes than was earlier so generally assumed. Nevertheless, the hypothesis that polyploidy was involved in the evolution of the Mantoidea must be advanced with reservations. In the first place, the chromosome numbers now known among mantids embrace nearly all intermediate values between the low and high peaks. Secondly, the photometric data here reported do not exclude the possibility of a differential polyteny in the spermatids of the different species considered. And finally, a change of great magnitude in the DNA content of spermatid nuclei has been established within a group of three congeneric species where the total evidence almost certainly excludes polyploidy. *Liturgousa actuosa* has approximately one and one half times the amount of DNA per spermatid that is found in *L. maya* and *L. cursor;* two changes of like nature and magnitude would result in a 2 : 1 ratio with no implication of polyploidy. The possibility of a polyploid relation between low and high number karyotypes suggested by the spermatid DNA ratio between *Pseudomiopteryx* and *Stagmomantis heterogamia* is, however, open to more critical tests which it is hoped to prosecute.

DNA values as subfamily characters

Aside from the detection of polyploid relationships, the utility of DNA determinations in cytotaxonomic analysis will depend largely on whether or not the lower categories such as subfamilies possess characteristic and distinguishable relative amounts. The present data, though stemming from far too few species to answer this question, are suggestive in relation to it. The subfamilies Pseudomiopteriginae and Manteinae, as here sampled, show a wide separation between the mean values of spermatid DNA, and there is no overlapping in the range of values obtained from the two groups; should these values prove characteristic for the subfamilies, they will constitute valid cytotaxonomic criteria. In the subfamily Liturgousinae, exclusive of *Liturgousa actuosa,* the mean amount of spermatid DNA differs significantly from that of the Manteinae on one side and from the Pseudomiopteriginae on the other, although in range of values there is wide overlapping. But *Liturgousa actuosa,* in which the mean amount of DNA per spermatid does not differ significantly from that of *Stagmomantis heterogamia,* bridges the gap between Liturgousinae and Manteinae. Since taxonomical and cytological evidence utterly preclude consideration of *Liturgousa actuosa* as a bridging form between these very distantly related subfamilies, this case alone sharply restricts the potential usefulness of the relative amount of DNA in the spermatid nucleus as a cytotaxonomic criterion.

Summary

1. The relative amount of DNA per spermatid nucleus has been determined by photometric microscopic measurement in eight species of mantids, and the results are discussed in relation to their cytology and the cytotaxonomic problems they present. The mantids studied are the following: Subfamily Liturgousinae—*Litur-*

gousa maya S. & Z., *L. actuosa* Rehn, *L. cursor* Rehn; Subfamily Choeradodinae —*Choeradodis rhombicollis* Latr.; Subfamily Manteinae—*Tauromantis championi* S. & Z., *Stagmomantis carolina* Johann, *S. heterogamia* S. & Z.; and Subfamily Pseudomiopteriginae—*Pseudomiopteryx infuscata* S. & Z.

2. Of the three closely similar species of *Liturgousa* tested, *L. maya* with 16 autosomes and *L. cursor* with 32 have the same content of DNA in the spermatid nucleus, confirming the cytological evidence that no polyploid relation exists between them. The greater diameter and greater total length of metaphase chromosomes in *L. maya* as compared with *L. cursor* remain unexplained.

3. *Liturgousa actuosa* has approximately one and one half times the amount of spermatid DNA as *L. maya* and *L. cursor,* in marked disagreement with the cytological evidence for an intermediate position.

4. *Tauromantis championi* and the two species of *Stagmomantis,* of the Manteinae, are uniform in DNA spermatid values, as in karyotypes. For *Choeradodis* no reliable species constant in nuclear DNA could be determined, due to abnormalities in the material, but a value not exceeding that of the Manteinae is indicated; this is in harmony with the cytological evidence.

5. The ratio of DNA per spermatid nucleus in *Pseudomiopteryx infuscata* to that in *Stagmomantis heterogamia* is 0.47; the ratio in total length of chromosomes at the preceding metaphase is 0.39. The implications of these findings for the hypothesis that polyploidy has been involved in the evolution of high and low number karyotypes among mantids are considered.

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